



Relationship of Space Use to Population Density in an Herbivorous Lizard

Allison C. Alberts

Herpetologica, Vol. 49, No. 4. (Dec., 1993), pp. 469-479.

Stable URL:

<http://links.jstor.org/sici?sici=0018-0831%28199312%2949%3A4%3C469%3AROSUTP%3E2.0.CO%3B2-0>

Herpetologica is currently published by Herpetologists' League.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/herpetologists.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

- DUVALL, D., K. M. SCUDDER, AND D. CHISZAR. 1980. Rattlesnake predatory behavior: Mediation of prey discrimination and release of swallowing by cues arising from envenomated mice. *Anim. Behav.* 28: 674-683.
- FURRY, K., T. SWAIN, AND D. CHISZAR. 1991. Strike-induced chemosensory searching and trail following by prairie rattlesnakes (*Crotalus viridis*) preying upon deer mice (*Peromyscus maniculatus*): Chemical discrimination among individual mice. *Herpetologica* 47:69-78.
- GANS, C., AND A. TAUB. 1964. Precautions for keeping poisonous snakes in captivity. *Curator* 7:196-205.
- HAYES, W. K. 1991. Envenomation Strategies of Prairie Rattlesnakes. Ph.D. Dissertation, University of Wyoming, Laramie, Wyoming.
- HAYES, W. K., AND J. G. GALUSHA. 1984. Effects of rattlesnake (*Crotalus viridis oregonus*) envenomation upon mobility of male wild and laboratory mice (*Mus musculus*). *Bull. Maryland Herpetol. Soc.* 20:135-144.
- KARDONG, K. V. 1986a. Predatory strike behavior of the rattlesnake, *Crotalus viridis oregonus*. *J. Comp. Psych.* 100:304-314.
- . 1986b. The rattlesnake strike. 1986. When things go amiss. *Copeia* 1986:816-820.
- KUHN, B. K., M. ROCHELLE, AND K. V. KARDONG. 1991. Effects of rattlesnake (*Crotalus viridis oregonus*) envenomation upon mobility and death rate of laboratory mice (*Mus musculus*) and wild mice (*Peromyscus maniculatus*). *Bull. Maryland Herpetol. Soc.* 27:189-200.
- LEWIS, D., AND C. J. BURKE. 1949. The use and misuse of the chi-square test. *Psychol. Bull.* 46:433-487.
- MELCER T., AND D. CHISZAR. 1989a. Strike-induced chemical preferences in prairie rattlesnakes (*Crotalus viridis*). *Anim. Learn. Behav.* 17:368-372.
- . 1989b. Striking prey creates a specific chemical search image in rattlesnakes. *Anim. Behav.* 37:477-486.
- ROBINSON, B. G., AND K. V. KARDONG. 1991. Relocation of struck prey by venomoid (venom-less) rattlesnakes, *Crotalus viridis oregonus*. *Bull. Maryland Herpetol. Soc.* 27:23-30.

Accepted: 14 December 1992
Associate Editor: H. Carl Gerhardt

Herpetologica, 49(4), 1993, 469-479
© 1993 by The Herpetologists' League, Inc.

RELATIONSHIP OF SPACE USE TO POPULATION DENSITY IN AN HERBIVOROUS LIZARD

ALLISON C. ALBERTS

*Center for Reproduction of Endangered Species, Zoological Society of San Diego,
P.O. Box 551, San Diego, CA 92112, USA*

ABSTRACT: Home ranges of desert iguanas, *Dipsosaurus dorsalis*, were compared during the breeding season at three localities that differed in adult population density. The abundance, richness, and diversity of plant resources varied across sites. Although home range size was not correlated with population density, increasing density was associated with greater home range overlap and a tendency for activity to be restricted to the home range interior. For both males and females, the level of home range advertisement, measured as the frequency of push-up displays, increased with increasing population density. The lack of a reciprocal relationship between population density and home range size may be a consequence of the non-uniform distribution of plants at the three sites. When increases in home range size do not produce linear increases in resources, as is the case for many herbivorous species, patterns of space use may be less related to population density per se than to the distribution of conspecifics and plant resources at a particular site.

Key words: Desert iguana; *Dipsosaurus*; Home range; Spatial dispersion; Population density

COLLECTIVE evidence on animal spacing suggests that the distribution of resources, whether they are food, shelter, or potential mates, ultimately affects dispersion, while the proximate mechanisms maintaining the arrangement of animals in space are behavioral (Brown and Orians,

1970; Crook, 1964; Davies and Lundberg, 1984; Lack, 1966). Optimality models have stressed that spatial distributions should reflect a balance between the benefits and costs of occupying a given area (Brown, 1964; Carpenter and MacMillen, 1976; Gill and Wolf, 1975; Pyke, 1979). Potential

benefits include obtaining resources, securing mates, and enhancing offspring survival, but they may be countered by increased energy expenditure, exposure to predators, and probability of injury during agonistic interactions (Rand, 1967). Game theoretic models have emphasized that the optimal amount of defended space should vary according to the level of defense shown by other members of the population (Maynard Smith, 1982; Parker, 1978). Both optimality and game theoretic models predict that patterns of space use will be determined by the relative value of resources to competitors and the relative costs accrued in defense of those resources.

Higher population density is expected to result in increased home range overlap in species that do not exhibit home range defense. When home ranges are defended, higher population density is more likely to produce a compression of home range size, in which each animal maintains exclusive access to resources, but controls a smaller area (Bradbury and Vehrencamp, 1976). In this case, intraspecific competition at high population density will limit the amount of space an animal can energetically afford to control, and an inverse relationship between population density and home range size is expected.

In general, male iguanid lizards exhibit some degree of home range defense, although both home range size and the intensity of aggressive behavior can vary widely among species (Stamps, 1977a, 1983). The prediction that home range size will be inversely related to population density has been made (Rand, 1967) and verified (Schoener and Schoener, 1980; Stamps, 1983) for some insectivorous iguanids but has not been systematically examined in herbivorous species. Although the availability of insect prey is relatively homogeneous in many environments, spatial and temporal variance in plant productivity can be high, especially in xeric habitats (Stamps, 1983). This non-uniform distribution of plant resources may lead to patterns of space use that are not predictable on the basis of population density alone. To assess the relationship between population density, resource distribution,

and home range use in an herbivorous iguanid, I studied spatial dispersion and the behavioral mechanisms contributing to spacing in three populations of desert iguanas, *Dipsosaurus dorsalis*, that differed in adult density.

MATERIALS AND METHODS

Study Sites

Desert iguanas were studied at three localities in the Coachella Valley, Riverside County, CA, during three breeding seasons (March–June) in 1986, 1987, and 1988 (Alberts, 1989). The sites were each 1 ha in area and differed in densities of adult desert iguanas (Table 1). The sites were isolated from each other by a freeway and urban development in the cities of Palm Springs and Thousand Palms, and the mean distance between sites was 8.0 km. Only one site was visited per day, and the three sites were visited sequentially, such that each site was visited every third day throughout most of each breeding season.

At all sites, I surveyed bushes greater than 0.5 m in aerial diameter. A total of 2482 individual plants belonging to 31 species were identified at the three sites. I used Simpson's index, a measure of the probability that any two individuals drawn at random belong to the same species, to calculate plant species diversity for each site (Simpson, 1949). The inverse of this index is positively correlated with species diversity. I chose this index because of the large numbers of relatively rare species found at the three sites, a factor that may lead to over estimates of diversity for some other commonly used indices (Peet, 1974).

Under the assumption that plants were roughly circular in cross section, I calculated percent cover for each species as the area covered by all bushes of that species >0.5 m in diameter. Bushes <0.5 m in aerial diameter are probably not used extensively by desert iguanas for shelter, although they may occasionally be used for food. Additionally, all plants >1 m tall were mapped using an optical range finder. Although this restriction limited the number of individual plants that were mapped to 327, it was difficult to obtain

TABLE 1.—Vegetation patterns at study sites with high, intermediate (Int), and low densities of desert iguanas. Diversity and patchiness indices are defined in the text.

	High	Int	Low
<i>Dipsosaurus</i> density (adults/ha)			
1986	34	23	12
1987	31	25	7
1988	35	20	12
Total number of plants	1059	614	809
Mean plant diameter (m)	0.74	0.58	0.76
Total % cover	7.10	2.80	7.20
Plant species richness	24	10	14
Plant diversity (1/Simpson D)	1.89	2.78	2.27
Lloyd's index of patchiness	1.13	0.96	1.37

accurate coordinates for plants <1 m tall. Despite its limitations, this methodology permitted a coarse comparison of the dispersion of large bushes at the three sites. From these data, I quantified the spatial distribution of large bushes using Lloyd's index of patchiness (= 1 for a random distribution, >1 for a clumped distribution, <1 for a uniform distribution) with a grid size of 20 m² (Lloyd, 1967).

Study Populations

Over the three breeding seasons, I noosed 96 adult desert iguanas and marked them with three small colored beads in unique color combinations sutured through the tail with surgical steel monofilament (Fisher and Muth, 1989), a technique that does not appear to interfere with natural behavior or adversely affect survivorship. Because each site was visited repeatedly over a long period of time, the measures in Table 1 reflect absolute rather than relative adult densities. Although unmarked juveniles were occasionally observed in the study sites after the initial capture and marking periods, unmarked adults were not.

Desert iguanas were sexed, weighed, and measured at the time of capture. Because most females were captured near the beginning of the breeding season in March and early April, their body masses probably do not reflect additional mass due to eggs, which do not develop until May or early June (Mayhew, 1971; Muth, 1980). I noted whether or not each desert iguana's

tail showed evidence of breakage and subsequent regeneration.

Home Range Measurements

Throughout the 1988 breeding season, I recorded positions of all marked desert iguanas to the nearest 1 m, relative to plants with known coordinates, by walking daily transects spanning the width of each site at 10-m intervals until the entire hectare and a 20-m margin on each side had been covered. All surveys were conducted between 0900 and 1400 h, the typical activity period of these lizards (Norris, 1953). I used both the convex polygon method (Rose, 1982) and a probabilistic technique yielding an estimate of the area encompassing 95% of the animal's total space utilization, termed the MAP (minimum area versus probability) estimate (Anderson, 1982), to calculate home range size. The latter method is nonparametric and therefore makes no assumptions about the underlying distribution of data points, and is relatively free from sample size bias.

I calculated polygon home range and MAP (0.95) estimates for the 51 desert iguanas for which enough sightings were obtained to estimate home range size reliably. Following Rose (1982), an analysis of home range size using chronologically increasing numbers of sightings was conducted for each of the 51 desert iguanas. Home range size initially increased with number of sightings but eventually revealed an asymptote at approximately 85% of the final estimated home range size when 12 or more sightings were used (Fig. 1).

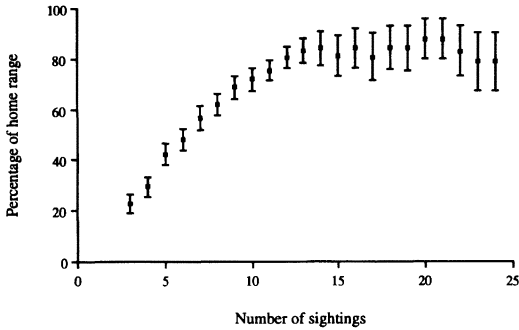


FIG. 1.—The relationship between number of sightings and mean percent of total convex polygon home range size for 51 desert iguanas. Standard errors are shown.

The mean number of sightings per lizard was 14.13 ± 1.42 at high density, 16.83 ± 2.85 at intermediate density, and 9.25 ± 1.52 at low density. Home range sizes should therefore be considered minimum estimates for desert iguanas at the low density site. For each polygon home range estimated, I determined the number of plants >1 m tall occurring within the home range boundaries and calculated the density of plants >1 m tall within each home range.

Home range overlap was estimated in two ways. To compare the overall degree of overlap at the three study sites, I calculated the total percent overlaps of (1) male home ranges with other male home ranges, (2) female home ranges with other female home ranges, and (3) male and female home ranges. Additionally, for those desert iguanas for which home ranges were estimated, I determined the number of male and female neighbors. For this analysis, desert iguanas with polygon home ranges that overlapped to any degree were defined as neighbors.

In order to estimate the intensity of home range advertisement at the three sites, I observed 20 males and 20 females (randomly chosen focal animals: six or seven individuals per site) for 30 min from a distance of 15 m with a 32-power field spotting scope. The numbers of push-up, or assertion, displays were recorded. Push-up displays, which are common in aggressive contexts (Carpenter, 1967), prob-

ably function in spatial advertisement and home range defense (Carpenter, 1961). I conducted all behavioral observations between 1100 and 1300 h, when desert iguanas were generally most active, during the 1988 breeding season.

Statistics

Two-way analysis of variance was employed to examine differences between the sexes and among the three study sites in home range size, number of bushes per home range, number of male and female neighbors, and the frequency of push-up displays. Hartley's test (Hartley, 1950; Sokal and Rohlf, 1981) revealed no significant heterogeneity of variances for these variables. However, for the MAP (0.95) home range data, it was necessary to perform a natural log transformation in order to meet assumptions of normality. In no case was a significant interaction between the sex and site variables found. Paired *t*-tests were used to compare polygon and MAP (0.95) home range estimates at the three sites. I used multiple regression to assess the independent effects of snout-vent length (SVL) and neighbor number on display frequency while controlling for correlations between them. A chi-square test was employed to compare the frequency of tail regeneration across study sites.

RESULTS

Plant resource distribution and lizard population density differed at the three study sites (Tables 1, 2). Within each site, the density of adult desert iguanas was constant within each season and showed moderate turnover from season to season. The mean recapture rate between years was 57.1% at low density, 60.0% at intermediate density, and 60.6% at high density. Adult sex ratio did not differ significantly from 1:1 at any site in any year. The frequency of regenerated tails differed at the three study sites ($\chi^2 = 7.06$, $df = 2$, $P = 0.03$), with the proportion of regenerated tails higher than expected at high density (22.5%), similar to expected at intermediate density (13.21%), and lower than expected at low density (3.03%).

TABLE 2.—Density per hectare of plant species at study sites with high, intermediate (Int), and low densities of desert iguanas. Percent cover for each species except those with <0.0001% cover is indicated in parentheses. Species with leaves or flowers identified as *Dipsosaurus dorsalis* food items by Mautz and Nagy (1987) are indicated by *. Plants that desert iguanas consumed during the present study are indicated by †.

Species	High	Int	Low
<i>Ambrosia dumosa</i> *†	751 (2.85)	—	495 (1.53)
<i>Psorothamnus schottii</i> *†	156 (1.90)	—	—
<i>P. arborescens</i>	—	328 (1.33)	—
<i>P. emoryi</i> *†	9 (0.06)	80 (0.40)	2 (0.004)
<i>Tiquilia palmeri</i> *	57 (0.04)	—	114 (0.08)
<i>T. plicata</i>	—	2 (0.003)	5 (0.003)
<i>Larrea tridentata</i> *†	38 (1.92)	9 (0.82)	164 (5.47)
<i>Hymenoclea salsola</i>	20 (0.19)	—	1 (0.004)
<i>Encelia farinosa</i>	16 (0.05)	—	—
<i>Atriplex canescens</i>	6 (0.06)	—	—
<i>Croton californicus</i> *	5 (0.004)	134 (0.08)	1 (0.002)
<i>Petalonyx thurberi</i>	1 (0.01)	57 (0.18)	—
<i>Astragalus lentiginosus</i>	—	4 (0.0003)	—
<i>Krameria parvifolia</i>	—	—	21 (0.06)
<i>Ephedra californica</i>	—	—	5 (0.005)
<i>Opuntia acanthocarpa</i>	—	—	1 (0.003)
<i>Brassica tournefortii</i> †	<0.0001%	<0.0001%	<0.0001%
<i>Camissonia claviformis</i> †	<0.0001%	<0.0001%	—
<i>Cryptantha angustifolia</i> †	<0.0001%	<0.0001%	<0.0001%
<i>Abronia villosa</i> †	<0.0001%	—	—
<i>Erodium texanum</i> †	—	—	<0.0001%
<i>Eriogonum inflatum</i>	<0.0001%	—	—
<i>E. deflexum</i>	<0.0001%	—	—
<i>Geraea canescens</i> *	<0.0001%	—	—
<i>Gilia latiflora</i>	<0.0001%	—	—
<i>Mentzelia involucrata</i>	<0.0001%	—	—
<i>Palafoxia linearis</i> *	<0.0001%	—	—
<i>Perityle emoryi</i>	<0.0001%	—	—
<i>Phacelia crenulata</i> †	<0.0001%	—	—
<i>Lotus</i> sp.	<0.0001%	—	<0.0001%
<i>Lupinus</i> sp.	<0.0001%	—	—

Plants had a slightly clumped distribution at the site with the highest density of desert iguanas. This site was dominated mostly by bur sage (*Ambrosia dumosa*) and to a lesser degree by indigo bush (*Psorothamnus schottii*). A variety of annuals also occurred at this site. Although this site supported the most individual plants and had the highest species richness, it had the lowest species diversity, primarily because the four most abundant species at this site accounted for 95% of all plants identified.

Plants at the site supporting an intermediate density of desert iguanas were more uniformly distributed than at the high and low density sites. The dominant plant species was Mojave dalea (*Psorothamnus arborescens*), a species completely absent from the other two sites. Dyeweed (*Psorothamnus emoryi*) was also relatively

common at this site. Although this site had the fewest and smallest plants, the least plant cover, and the lowest plant species richness, it had the highest plant species diversity.

Plants at the site with lowest desert iguana density had a clumped distribution. This site was dominated by two species, bur sage and creosote (*Larrea tridentata*). Although intermediate in species richness, diversity, and number of individual plants, this site exhibited the greatest percent cover, because many of the individual creosote bushes were very large. Although creosote was present at all of the sites, it was most prevalent at this site.

Based on MAP (0.95) utilization estimates, home range size differed significantly at the three sites ($F = 4.67$, $df = 2,45$, $P = 0.01$). Home ranges of both sexes

TABLE 3.—Morphological measurements, home range size estimates, number of large bushes per home range, percent overlap of home ranges, number of neighbors, and display frequencies (mean \pm 1 SE) for male and female desert iguanas at high, intermediate (Int), and low population density. Desert iguanas with convex polygon home ranges that overlapped to any degree were defined as neighbors.

	Males			Females		
	High	Int	Low	High	Int	Low
I. Morphology						
Mass (g)	60.5 \pm 1.9	59.2 \pm 1.5	54.0 \pm 2.7	50.2 \pm 2.0	46.3 \pm 1.5	42.7 \pm 1.2
SVL (cm)	11.9 \pm 0.1	11.5 \pm 0.1	11.8 \pm 0.2	11.3 \pm 0.1	10.9 \pm 0.1	10.8 \pm 0.1
II. Home range size						
Polygon (m ²)	592 \pm 123	585 \pm 176	153 \pm 126	270 \pm 82	310 \pm 158	65 \pm 28
MAP (0.95) (m ²)	427 \pm 69	738 \pm 218	189 \pm 24	216 \pm 47	229 \pm 32	79 \pm 47
Plants/home range	7.6 \pm 1.5	2.1 \pm 0.7	10.0 \pm 2.0	3.0 \pm 0.6	1.7 \pm 0.7	3.5 \pm 0.8
III. Home range overlap						
% Overlap males	36.99%	7.47%	0.00%	35.44%	1.14%	12.85%
% Overlap females	35.44%	1.14%	12.85%	12.19%	0.00%	1.41%
Male neighbors	2.8 \pm 0.4	1.3 \pm 0.2	0.0 \pm 0.0	3.0 \pm 0.4	1.3 \pm 0.9	0.8 \pm 0.2
Female neighbors	3.0 \pm 0.5	0.7 \pm 0.3	2.5 \pm 0.5	1.4 \pm 0.4	0.3 \pm 0.3	0.5 \pm 0.2
IV. Home range advertisement						
Displays/0.5 h	68.9 \pm 18.2	45.0 \pm 38.9	0.0 \pm 0.0	11.8 \pm 2.3	1.4 \pm 2.2	0.0 \pm 0.0

were largest at the site with the intermediate density of desert iguanas and smallest at the site with the low density of desert iguanas (Table 3). At all sites, home ranges of males were larger than those of females ($F = 9.70$, $df = 1,45$, $P = 0.003$). If data are based on an inadequate number of sightings, polygon methods can underestimate home range sizes compared to probabilistic techniques (Waldschmidt, 1979). In the present study, polygon estimates for desert iguana home ranges tended to exceed 95% utilization estimates at the site with high desert iguana density (paired $t = 1.85$, $df = 30$, $P = 0.07$) (Table 3). This is expected if individuals spend most of their time in a central, core area of the home range, but make infrequent forays beyond the region of usual activity. Alternatively, if the two estimates coincide, activity at the boundaries is relatively frequent compared to activity in the interior. No difference between polygon and MAP (0.95) estimates was found at low (paired $t = 0.89$, $df = 11$, $P = 0.39$) or intermediate (paired $t = 0.57$, $df = 7$, $P = 0.57$) densities of desert iguanas.

The number of plants >1 m tall per home range differed both between the sexes ($F = 3.33$, $df = 1,45$, $P = 0.05$) and among sites ($F = 6.70$, $df = 2,45$, $P = 0.01$). At all sites, male home ranges contained more plants than female home ranges. The density of plants (number of plants >1 m tall/m²) was not significantly different for male and female home ranges ($F = 0.0003$, $df = 1,45$, $P = 0.99$), suggesting that male home ranges contain more plants primarily because they are larger. Regardless of sex, desert iguanas at the sites with high and low population densities occupied home ranges that contained more plants than those at the site with intermediate population density (Table 3). However, the density of plants per home range was also much lower at the site with the intermediate density of desert iguanas ($F = 7.38$, $df = 2,45$, $P = 0.002$), indicating that differences in plant abundance and distribution influence the number of plants per home range at the three sites.

High spatial overlap of home ranges occurred both within and between the sexes

at high population density, although it was lowest between females. At intermediate population density, moderate overlap between males, no overlap between females, and slight overlap between the sexes existed. Moderate overlap between the sexes, no overlap between males, and slight overlap between females was found at low population density (Table 3). The number of male neighbors per individual differed among the three sites ($F = 11.17$, $df = 2,45$, $P = 0.0001$), increasing at higher population density. Across sites, the number of male neighbors per individual was similar for males and females ($F = 0.48$, $df = 1,45$, $P = 0.83$). The pattern was slightly different for number of female neighbors. Although the number of female neighbors also increased with increasing population density ($F = 5.02$, $df = 2,45$, $P = 0.01$), males at all sites had more female neighbors than did females ($F = 5.87$, $df = 1,45$, $P = 0.02$).

At all sites, males performed more push-up displays than females ($F = 5.89$, $df = 1,34$, $P = 0.02$). There was a tendency for display frequency to increase with increasing population density in both sexes ($F = 2.85$, $df = 2,34$, $P = 0.07$), and at low population density, no adult desert iguana of either sex was observed to display (Table 3). For 35 individuals, data on both display frequency and home range size were available. Snout-vent length and number of male neighbors together explained a small but marginally significant proportion of variance in the display rates of males ($R^2 = 0.17$, $df = 17$, $P = 0.10$); SVL ($t = 2.22$, $P = 0.04$), but not number of male neighbors ($t = 0.24$, $P = 0.81$), emerged as a significant predictor of male display rate. The pattern differed for females, in which display frequency was somewhat better explained by SVL and number of female neighbors ($R^2 = 0.30$, $df = 16$, $P = 0.03$), and number of neighbors ($t = 1.90$, $P = 0.08$) was a stronger predictor of female display rate than SVL ($t = 1.43$, $P = 0.17$).

DISCUSSION

Plants are essential to desert iguanas both as a primary food source (Mautz and Nagy, 1987; Minnich and Shoemaker, 1970) and

because they provide space for the construction of burrows among their roots (Norris, 1953). In this study, sites supporting different densities of desert iguanas were characterized by variation in the identity, diversity, richness, and spatial distribution of plant resources. Whereas mean plant size was similar across sites, both plant species richness and the abundance of individual plants differed considerably. Variation in plant species diversity and in the degree of spatial uniformity of plants was also evident, though less dramatic. Although temporal fluctuation in plant availability was not examined in the present study, Krekorian (1976) showed that periodic storms can have a strong influence on leaf availability and hence movement patterns of desert iguanas.

Variation in the temporal and spatial distribution of plant resources, especially preferred food items such as fruits and flowers, has been described for several of the herbivorous iguanids (Berry, 1974; Iverson, 1979; Krekorian, 1984; Nagy, 1973; Werner, 1982) and may contribute to variability in social organization both within and between species (Dugan and Wiewandt, 1982; Ryan, 1982). That desert iguanas vigorously defend home ranges during the breeding season at some localities (Norris, 1953), yet exhibit extensive home range overlap and a relative lack of aggression at others (Krekorian, 1983), likely results at least in part from differences in the distribution and abundance of plant resources available to individual desert iguanas. In contrast, the insect prey of many of the smaller iguanids are more uniformly distributed and show less temporal fluctuation within, although not necessarily between, seasons (Ballinger, 1977; Dunham, 1978; Stamps et al., 1981). This relatively homogeneous resource base may explain the widespread existence of aggressive home range defense among insectivorous iguanids (Stamps, 1977a).

In the present study, home ranges of desert iguanas at low population density, especially those of females, tended to be smaller than at higher density. This result differs from certain insectivorous iguanids, in which home range size varies inversely

with population density (Schoener and Schoener, 1980) and food abundance (Simon, 1975). In my study, plant resources at the site with the low density of desert iguanas were moderately abundant and clumped. Although this site was intermediate in plant abundance, desert iguana home ranges contained more large bushes than at the higher population density sites. This indicates that despite their relatively small area, home ranges at this site were positioned such that they overlapped available plant resources. Although the home range of each male overlapped those of 2–3 females, the non-uniform distribution of plants at this site resulted in relatively small, widely distributed, and non-overlapping male home ranges.

Higher population densities in insectivorous iguanids often result in a reduction in home range size, presumably because of the rising costs of defense (Rand, 1967; Schoener and Schoener, 1980). For desert iguanas, home range size showed an increase rather than a decrease at the higher population density sites. At the site with the intermediate density of desert iguanas, this increase was probably directly related to the relatively low abundance and fairly uniform distribution of plant resources. Despite larger home range size, the number of large bushes per home range was substantially lower than at the site with the low density of desert iguanas. Relatively low home range overlap both within and between the sexes at this site may reflect the need for desert iguanas to maintain exclusive access to a minimum amount of plant material. Home range size at the site with the high density of desert iguanas, where plant productivity was highest in both species richness and bush abundance, was also larger than at the low density site. The somewhat clumped distribution of plants, combined with the high density of desert iguanas, apparently has not resulted in a compression of home range size, but in extensive home range overlap. While not readily predictable on the basis of population density alone, home range use by desert iguanas does appear to be influenced by both the distribution and abundance of plant resources.

In addition to patterns of home range size and overlap, the level of home range advertisement varied across sites. No push-up displays were observed among desert iguanas of either sex at the site where population density was low. Although the existence of non-contiguous male home ranges may preclude the need for high levels of home range advertisement, it is difficult to determine whether the tendency for desert iguanas to behave aggressively is lower at low population density, or if the opportunities for lizards to interact simply occur less often. In another iguanid, *Sceloporus merriami*, few contacts between individuals occurred at low population densities, but intense display was observed on the rare occasions when males did meet (Milstead, 1970).

As the density of desert iguanas increased, the frequency of push-up displays increased. The proportion of regenerated tails was also greater at higher population density. Tail loss in lizards can result from failed predation attempts but may additionally reflect the intensity of social aggression (Fox et al., 1981; Parker and Pianka, 1973; Vitt et al., 1974). In desert iguanas, conspecific fighting can lead to broken tails (Carpenter, 1967; Norris, 1953). Similar yearly recapture rates at the three study sites suggest that the higher proportion of regenerated tails at the high population density site may result from differences in aggressive behavior rather than predation regime. In another iguana, *Cyclura stejnegeri*, aggressive interactions also occurred more often at higher population density (Dugan and Wiewandt, 1982). For desert iguanas at high density, higher levels of aggression combined with extensive home range overlap may confine activity to the interior of the home range. The areas in which individuals spent 95% of their time were smaller than the polygon home range estimates at this site, indicating that most activity occurred well within the home range boundaries. Apparently, home range defense is not abandoned at high population density but may be restricted to a core area of the home range where overlap with conspecifics is lower. Results from all three sites

indicate that the degree and nature of aggressive behavior can be highly variable across desert iguana populations when variation in the underlying resource base exists.

Regardless of population density, consistent differences between male and female desert iguanas in several features of home range use and advertisement were found. Males occupied larger home ranges than did females. Although there are exceptions (Boag, 1973; Dugan, 1982), this pattern has been documented for many other species of both insectivorous and herbivorous lizards (Ferner, 1974; Nagy, 1973; Rose, 1982). Additionally, body size had an important influence on the level of home range advertisement in male desert iguanas. Home ranges in male lizards are often larger than would be expected based solely on energetic considerations (Rose, 1982), and it has been proposed that the primary purpose of home range defense in males is to increase access to potential mates rather than to maintain exclusive access to limited food resources (Ryan, 1982; Schoener and Schoener, 1980; Stamps, 1977b).

In my study, female desert iguanas had fewer female neighbors than males, but the number of female neighbors influenced female display rate. For desert iguanas, female home ranges must contain some minimum amount of plant material for successful reproduction to occur, both because females need adequate food to withstand the energetic demands of egg laying, and also because hatchlings, which remain close to their hatching site (Krekorian, 1984), may require high quality food to survive. At high population density, where the available food supply is shared by many individuals, female desert iguanas may increase their level of home range advertisement in order to meet these energy requirements. While they do not constitute an adequate test of the hypothesis that female spacing patterns are affected primarily by food supply and male spacing patterns by access to potential mates, results for desert iguanas are consistent with this theory.

In two comprehensive reviews, Stamps (1977a, 1983) proposed that the more

patchy distribution of plant resources relative to insects contributes to substantial behavioral flexibility in patterns of space utilization among herbivorous iguanids. Results of my study indicate that variability in home range size and advertisement in desert iguanas may not be readily predictable without specific knowledge regarding the abundance and distribution of plant resources at a given site. In order to assess further the relationships between space use, population density, and resource distribution in iguanid lizards, it may prove especially useful to concentrate on species such as *Ctenosaura similis*, which exhibit an ontogenetic shift in diet from insects to plants (Montanucci, 1968), or to compare closely related species such as *Brachylophus fasciatus*, which has a mixed diet of insects and plants, and *B. vitiensis*, which is entirely herbivorous (Gibbons and Watkins, 1982).

Acknowledgments.—I am grateful to J. Bradbury for guidance and advice on all aspects of the project, A. Muth and M. Fisher at University of California Deep Canyon Desert Research Center for invaluable logistical support, and D. Bolger, C. Booth, N. Burns, C. Thompson, and A. Alberts for field assistance. J. Bradbury provided computer programs to calculate polygon and Anderson home ranges. J. Bradbury, D. Bolger, N. Burns, A. Muth, J. Phillips, T. Price, and anonymous reviewers provided critical comments on the manuscript. This research was conducted while the author was a doctoral student in the Biology Department at the University of California, San Diego, and was partially funded by a training grant from the National Institutes of Health.

LITERATURE CITED

- ALBERTS, A. C. 1989. The Evolution of Chemical Signalling in the Desert Iguana, *Dipsosaurus dorsalis*. Ph.D. Dissertation, University of California, San Diego, La Jolla, California.
- ANDERSON, D. J. 1982. The home range: A new nonparametric estimation technique. *Ecology* 63: 103-112.
- BALLINGER, R. E. 1977. Reproductive strategies: Food availability as a source of proximal variation in a lizard. *Ecology* 58:628-635.
- BERRY, K. H. 1974. The ecology and social behavior of the chuckwalla, *Sauromalus obesus obesus* Baird. Univ. California Publ. Zool. 101:1-60.
- BOAG, D. A. 1973. Spatial relationships among members of a population of wall lizards. *Oecologia* 12:1-13.
- BRADBURY, J. W., AND S. L. VEHCAMP. 1976. Social organization and foraging in Emballonurid

- bats. II. A model for the determination of group size. *Behav. Ecol. Sociobiol.* 1:383-404.
- BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 76:160-169.
- BROWN, J. L., AND G. H. ORIANI. 1970. Spacing patterns in mobile animals. *Ann. Rev. Ecol. Syst.* 1:239-257.
- CARPENTER, C. C. 1961. Patterns of social behavior in the desert iguana, *Dipsosaurus dorsalis*. *Copeia* 1961:396-405.
- . 1967. Aggression and social structure in iguanid lizards. Pp. 87-105. *In* W. W. Milstead (Ed.), *Lizard Ecology: A Symposium*. University of Missouri Press, Columbia, Missouri.
- CARPENTER, F. L., AND F. E. MACMILLEN. 1976. Threshold model of feeding territoriality and test with a Hawaiian honey creeper. *Science* 194:639-642.
- CROOK, J. H. 1964. The adaptive significance of avian social organizations. *Symp. Zool. Soc. Lond.* 14:181-218.
- DAVIES, N. B., AND A. LUNDBERG. 1984. Food distribution and variable mating system in the dunnoek, *Prunella modularis*. *J. Anim. Ecol.* 53:895-912.
- DUGAN, B. 1982. The mating behavior of the green iguana, *Iguana iguana*. Pp. 320-341. *In* G. M. Burghardt and A. S. Rand (Eds.), *Iguanas of the World*. Noyes, Park Ridge, New Jersey.
- DUGAN, B., AND T. V. WIEWANDT. 1982. Sociological determinants of mating strategies in iguanine lizards. Pp. 303-319. *In* G. M. Burghardt and A. S. Rand (Eds.), *Iguanas of the World*. Noyes, Park Ridge, New Jersey.
- DUNHAM, A. E. 1978. Food availability as a proximate factor influencing individual growth rates in the iguanid lizard *Sceloporus merriami*. *Ecology* 59:770-778.
- FERNER, J. W. 1974. Home range size and overlap in *Sceloporus undulatus erythrocheilus* (Reptilia: Iguanidae). *Copeia* 1974:332-337.
- FISHER, M., AND A. MUTH. 1989. A technique for permanently marking lizards. *Herpetol. Rev.* 20:45-46.
- FOX, S. F., E. ROSE, AND R. MYERS. 1981. Dominance and the acquisition of superior home ranges in the lizard *Uta stansburiana*. *Ecology* 62:888-893.
- GIBBONS, J. R. H., AND I. F. WATKINS. 1982. Behavior, ecology, and conservation of South Pacific banded iguanas, *Brachylophus*, including a newly discovered species. Pp. 418-441. *In* G. M. Burghardt and A. S. Rand (Eds.), *Iguanas of the World*. Noyes, Park Ridge, New Jersey.
- GILL, F. B., AND L. L. WOLF. 1975. Economics of feeding territoriality in the golden-winged sunbird. *Ecology* 56:333-345.
- HARTLEY, H. O. 1950. The maximum F-ratio as a shortcut test for heterogeneity of variances. *Biometrika* 37:308-312.
- IVERSON, J. B. 1979. Behavior and ecology of the rock iguana, *Cyclura carinata*. *Bull. Florida St. Mus. Biol. Sci.* 24:175-358.
- KREKORIAN, C. O. 1976. Home range size and overlap and their relationship to food abundance in the desert iguana, *Dipsosaurus dorsalis*. *Herpetologica* 32:405-412.
- . 1983. Population density of the desert iguana, *Dipsosaurus dorsalis* (Reptilia: Iguanidae), in southern California. *Copeia* 1983:268-271.
- . 1984. Life history of the desert iguana, *Dipsosaurus dorsalis*. *Herpetologica* 40:415-424.
- LACK, D. 1966. *Population Studies of Birds*. Clarendon Press, Oxford, United Kingdom.
- LLOYD, M. 1967. Mean crowding. *J. Anim. Ecol.* 36:1-30.
- MAUTZ, W. J., AND K. A. NAGY. 1987. Ontogenetic changes in diet, field metabolic rate, and water turnover in the herbivorous lizard *Dipsosaurus dorsalis*. *Physiol. Zool.* 60:640-658.
- MAYHEW, W. W. 1971. Reproduction in the desert lizard, *Dipsosaurus dorsalis*. *Herpetologica* 27:57-77.
- MAYNARD SMITH, J. 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge, United Kingdom.
- MILSTEAD, W. W. 1970. Late summer behavior of the lizards *Sceloporus merriami* and *Urosaurus ornatus* in the field. *Herpetologica* 26:343-354.
- MINNICH, J. E., AND V. H. SHOEMAKER. 1970. Diet, behavior, and water turnover in the desert iguana, *Dipsosaurus dorsalis*. *Am. Midl. Nat.* 84:496-509.
- MONTANUCCI, R. R. 1968. Comparative dentition in four iguanid lizards. *Herpetologica* 24:305-315.
- MUTH, A. 1980. Physiological ecology of desert iguana (*Dipsosaurus dorsalis*) eggs: Temperature and water relations. *Ecology* 61:1335-1343.
- NAGY, K. A. 1973. Behavior, diet and reproduction in a desert lizard, *Sauromalus obesus*. *Copeia* 1973:93-102.
- NORRIS, K. S. 1953. The ecology of the desert iguana, *Dipsosaurus dorsalis*. *Ecology* 34:265-287.
- PARKER, G. A. 1978. Evolutionarily stable strategies. Pp. 30-61. *In* J. R. Krebs and N. B. Davies (Eds.), *Behavioural Ecology: An Evolutionary Approach*, 2nd ed. Blackwell Scientific Publications, Oxford, United Kingdom.
- PARKER, W. S., AND E. R. PIANKA. 1973. Notes on the ecology of the iguanid lizard *Sceloporus magister*. *Herpetologica* 29:143-152.
- PEET, R. K. 1974. The measurement of species diversity. *Ann. Rev. Ecol. Syst.* 5:285-307.
- PYKE, G. H. 1979. The economics of territory size and time budget in the golden-winged sunbird. *Am. Nat.* 114:131-145.
- RAND, A. S. 1967. The adaptive significance of territoriality in iguanid lizards. Pp. 106-115. *In* W. W. Milstead (Ed.), *Lizard Ecology: A Symposium*. University of Missouri Press, Columbia, Missouri.
- ROSE, B. 1982. Lizard home ranges: Methodology and functions. *J. Herpetol.* 16:253-269.
- RYAN, M. J. 1982. Variation in iguanine social organization: Mating systems in chuckwallas (*Sauromalus*). Pp. 380-390. *In* G. M. Burghardt and A. S. Rand (Eds.), *Iguanas of the World*. Noyes, Park Ridge, New Jersey.
- SCHOENER, T. W., AND A. SCHOENER. 1980. Densities, sex ratios, and population structure in four

- species of Bahamian *Anolis* lizards. *J. Anim. Ecol.* 49:19–53.
- SIMON, C. A. 1975. The influence of food abundance on territory size in the iguanid lizard *Sceloporus jarrovi*. *Ecology* 56:993–998.
- SIMPSON, E. H. 1949. Measurement of diversity. *Nature* 163:688.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. W. H. Freeman, San Francisco.
- STAMPS, J. A. 1977a. Social behavior and spacing patterns in lizards. Pp. 265–334. *In* C. Gans and D. W. Tinkle (Eds.), *Biology of the Reptilia*, Vol 7. Academic Press, New York.
- . 1977b. The relationship between resource competition, risk, and aggression in a tropical territorial lizard. *Ecology* 58:349–358.
- . 1983. Sexual selection, sexual dimorphism, and territoriality. Pp. 169–204. *In* R. B. Huey, E. R. Pianka, and T. W. Schoener (Eds.), *Lizard Ecology: Studies of a Model Organism*. Harvard University Press, Cambridge, Massachusetts.
- STAMPS, J. A., S. TANAKA, AND V. V. KRISHNAN. 1981. The relationship between selectivity and food abundance in a juvenile lizard. *Ecology* 62:1079–1092.
- VITT, L. J., J. D. CONGDON, A. C. HULSE, AND J. E. PLATZ. 1974. Territorial aggressive encounters and tail breaks in the lizard *Sceloporus magister*. *Copeia* 1974:990–993.
- WALDSCHMIDT, S. R. 1979. The effect of statistically based models on home range size estimate in *Uta stansburiana*. *Am. Midl. Nat.* 101:236–240.
- WERNER, D. I. 1982. Social organization and ecology of land iguanas, *Conolophus subcristatus*, on Isla Fernandina, Galapagos. Pp. 342–356. *In* G. M. Burghardt and A. S. Rand (Eds.), *Iguanas of the World*. Noyes, Park Ridge, New Jersey.

Accepted: 19 December 1992

Associate Editor: Daniel Formanowicz, Jr.

Herpetologica, 49(4), 1993, 479–487
© 1993 by The Herpetologists' League, Inc.

NESTING OF *PSEUDEMYDURA UMBRINA* (TESTUDINES: CHELIDAE): THE OTHER WAY ROUND

GERALD KUCHLING

*Department of Zoology, The University of Western Australia,
Perth, WA 6009, Australia*

ABSTRACT: *Pseudemydura umbrina* nests in full daylight and typically during rain-bearing, low pressure weather fronts. The nesting action pattern of *P. umbrina* is unique because the nest cavity is constructed with the forelegs, with the female being head-down in the hole; during this stage, the hindlegs are only used to push soil material, which accumulates beside the female, behind and out of the hole. Nest digging in *P. umbrina* may have evolved from the typical turtle nesting pattern by an alteration and expansion of the stage of nest site preparation, which now incorporates the actual digging of the nest chamber, and a drastic reduction, or omission, of the typical stage of digging the egg cavity with the hindlegs. The other stages of nesting in *P. umbrina* follow the well-defined sequence of steps of chelonian nesting.

Key words: Nesting; Digging; Nest cavity; Egg laying; Stereotyped behavior; Australia; Testudines; Chelidae; *Pseudemydura umbrina*

TURTLE nesting usually follows a well defined sequence of steps that have been behaviorally characterised and interspecifically compared. Commonly distinguished phases are nest site selection, preparation of the nest site, digging the nest hole (egg cavity), oviposition, and filling in and covering the nest (Ehrenfeld, 1979; Hailmann and Elowson, 1992). In the case

of aquatic turtles, nesting generally occurs on dry land and involves the movement from the aquatic to the terrestrial habitat.

Turtles occupy diverse climatic zones and habitats, and it is not surprising that the criteria for nest site selection are broad and the associated behaviors flexible. With the next steps, the interspecific variability becomes progressively reduced. Typically,

LINKED CITATIONS

- Page 1 of 5 -



You have printed the following article:

Relationship of Space Use to Population Density in an Herbivorous Lizard

Allison C. Alberts

Herpetologica, Vol. 49, No. 4. (Dec., 1993), pp. 469-479.

Stable URL:

<http://links.jstor.org/sici?sici=0018-0831%28199312%2949%3A4%3C469%3AROSUTP%3E2.0.CO%3B2-0>

This article references the following linked citations. If you are trying to access articles from an off-campus location, you may be required to first logon via your library web site to access JSTOR. Please visit your library's website or contact a librarian to learn about options for remote access to JSTOR.

Literature Cited

The Home Range: A New Nonparametric Estimation Technique

D. John Anderson

Ecology, Vol. 63, No. 1. (Feb., 1982), pp. 103-112.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28198202%2963%3A1%3C103%3ATHRANN%3E2.0.CO%3B2-X>

Reproductive Strategies: Food Availability as a Source of Proximal Variation in a Lizard

Royce E. Ballinger

Ecology, Vol. 58, No. 3. (Late Spring, 1977), pp. 628-635.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28197721%2958%3A3%3C628%3ARSFAAA%3E2.0.CO%3B2-X>

Spacing Patterns in Mobile Animals

Jerram L. Brown; Gordon H. Orians

Annual Review of Ecology and Systematics, Vol. 1. (1970), pp. 239-262.

Stable URL:

<http://links.jstor.org/sici?sici=0066-4162%281970%291%3C239%3ASPIMA%3E2.0.CO%3B2-9>

Patterns of Social Behavior in the Desert Iguana, *Dipsosaurus dorsalis*

Charles C. Carpenter

Copeia, Vol. 1961, No. 4. (Dec. 19, 1961), pp. 396-405.

Stable URL:

<http://links.jstor.org/sici?sici=0045-8511%2819611219%293%3A1961%3A4%3C396%3APOSBIT%3E2.0.CO%3B2-7>

LINKED CITATIONS

- Page 2 of 5 -



Threshold Model of Feeding Territoriality and Test with a Hawaiian Honeycreeper

F. L. Carpenter; R. E. MacMillen

Science, New Series, Vol. 194, No. 4265. (Nov. 5, 1976), pp. 639-642.

Stable URL:

<http://links.jstor.org/sici?sici=0036-8075%2819761105%293%3A194%3A4265%3C639%3ATMOFTA%3E2.0.CO%3B2-C>

Food Distribution and a Variable Mating System in the Dunnock, *Prunella modularis*

N. B. Davies; A. Lundberg

The Journal of Animal Ecology, Vol. 53, No. 3. (Oct., 1984), pp. 895-912.

Stable URL:

<http://links.jstor.org/sici?sici=0021-8790%28198410%2953%3A3%3C895%3AFDAAVM%3E2.0.CO%3B2-Z>

Food Availability as a Proximate Factor Influencing Individual Growth Rates in the Iguanid Lizard *Sceloporus Merriami*

Arthur E. Dunham

Ecology, Vol. 59, No. 4. (Summer, 1978), pp. 770-778.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28197822%2959%3A4%3C770%3AFAAAPF%3E2.0.CO%3B2-L>

Home-Range Size and Overlap in *Sceloporus undulatus erythrocheilus* (Reptilia: Iguanidae)

John W. Ferner

Copeia, Vol. 1974, No. 2. (Jun. 13, 1974), pp. 332-337.

Stable URL:

<http://links.jstor.org/sici?sici=0045-8511%2819740613%293%3A1974%3A2%3C332%3AHSOIS%3E2.0.CO%3B2-0>

Dominance and the Acquisition of Superior Home Ranges in the Lizard *Uta Stansburiana*

Stanley F. Fox; Elizabeth Rose; Ronald Myers

Ecology, Vol. 62, No. 4. (Aug., 1981), pp. 888-893.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28198108%2962%3A4%3C888%3ADATAOS%3E2.0.CO%3B2-%23>

Economics of Feeding Territoriality in the Golden-Winged Sunbird

Frank B. Gill; Larry L. Wolf

Ecology, Vol. 56, No. 2. (Early Spring, 1975), pp. 333-345.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28197521%2956%3A2%3C333%3AEOFIT%3E2.0.CO%3B2-O>

LINKED CITATIONS

- Page 3 of 5 -



The Maximum F-Ratio as a Short-Cut Test for Heterogeneity of Variance

H. O. Hartley

Biometrika, Vol. 37, No. 3/4. (Dec., 1950), pp. 308-312.

Stable URL:

<http://links.jstor.org/sici?sici=0006-3444%28195012%2937%3A3%2F4%3C308%3ATMAAST%3E2.0.CO%3B2-V>

Population Density of the Desert Iguana, *Dipsosaurus dorsalis* (Reptilia: Iguanidae), in Southern California

C. O'Neil Kerkorian

Copeia, Vol. 1983, No. 1. (Feb. 10, 1983), pp. 268-271.

Stable URL:

<http://links.jstor.org/sici?sici=0045-8511%2819830210%293%3A1983%3A1%3C268%3APDOTDI%3E2.0.CO%3B2-E>

'Mean Crowding'

Monte Lloyd

The Journal of Animal Ecology, Vol. 36, No. 1. (Feb., 1967), pp. 1-30.

Stable URL:

<http://links.jstor.org/sici?sici=0021-8790%28196702%2936%3A1%3C1%3A%60C%3E2.0.CO%3B2-1>

Physiological Ecology of Desert Iguana (*Dipsosaurus Dorsalis*) Eggs: Temperature and Water Relations

Allan Muth

Ecology, Vol. 61, No. 6. (Dec., 1980), pp. 1335-1343.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28198012%2961%3A6%3C1335%3APEODI%28%3E2.0.CO%3B2-T>

Behavior, Diet and Reproduction in a Desert Lizard, *Sauromalus obesus*

Kenneth A. Nagy

Copeia, Vol. 1973, No. 1. (Mar. 5, 1973), pp. 93-102.

Stable URL:

<http://links.jstor.org/sici?sici=0045-8511%2819730305%293%3A1973%3A1%3C93%3ABDARIA%3E2.0.CO%3B2-6>

The Ecology of the Desert Iguana *Dipsosaurus Dorsalis*

Kenneth S. Norris

Ecology, Vol. 34, No. 2. (Apr., 1953), pp. 265-287.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28195304%2934%3A2%3C265%3ATEOTDI%3E2.0.CO%3B2-U>

LINKED CITATIONS

- Page 4 of 5 -



The Measurement of Species Diversity

Robert K. Peet

Annual Review of Ecology and Systematics, Vol. 5. (1974), pp. 285-307.

Stable URL:

<http://links.jstor.org/sici?sici=0066-4162%281974%295%3C285%3ATMOSD%3E2.0.CO%3B2-X>

The Economics of Territory Size and Time Budget in the Golden-Winged Sunbird

Graham H. Pyke

The American Naturalist, Vol. 114, No. 1. (Jul., 1979), pp. 131-145.

Stable URL:

<http://links.jstor.org/sici?sici=0003-0147%28197907%29114%3A1%3C131%3ATEOTSA%3E2.0.CO%3B2-O>

Lizard Home Ranges: Methodology and Functions

Barbara Rose

Journal of Herpetology, Vol. 16, No. 3. (Sep., 1982), pp. 253-269.

Stable URL:

<http://links.jstor.org/sici?sici=0022-1511%28198209%2916%3A3%3C253%3ALHRMAF%3E2.0.CO%3B2-L>

Densities, Sex Ratios, and Population Structure in Four Species of Bahamian Anolis Lizards

Thomas W. Schoener; Amy Schoener

The Journal of Animal Ecology, Vol. 49, No. 1. (Feb., 1980), pp. 19-53.

Stable URL:

<http://links.jstor.org/sici?sici=0021-8790%28198002%2949%3A1%3C19%3ADSRAPS%3E2.0.CO%3B2-5>

The Influence of Food Abundance on Territory Size in the Iguanid Lizard *Sceloporus jarrovi*

Carol A. Simon

Ecology, Vol. 56, No. 4. (Jul., 1975), pp. 993-998.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28197507%2956%3A4%3C993%3ATIOFAO%3E2.0.CO%3B2-4>

The Relationship between Resource Competition, Risk, and Aggression in a Tropical Territorial Lizard

J. A. Stamps

Ecology, Vol. 58, No. 2. (Mar., 1977), pp. 349-358.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28197703%2958%3A2%3C349%3ATRBRCR%3E2.0.CO%3B2-1>

LINKED CITATIONS

- Page 5 of 5 -



The Relationship between Selectivity and Food Abundance in a Juvenile Lizard

Judy Stamps; Sanford Tanaka; V. V. Krishnan

Ecology, Vol. 62, No. 4. (Aug., 1981), pp. 1079-1092.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28198108%2962%3A4%3C1079%3ATRBSAF%3E2.0.CO%3B2-B>

Territorial Aggressive Encounters and Tail Breaks in the Lizard *Sceloporus magister*

Laurie J. Vitt; Justin D. Congdon; Arthur C. Hulse; James E. Platz

Copeia, Vol. 1974, No. 4. (Dec. 31, 1974), pp. 990-993.

Stable URL:

<http://links.jstor.org/sici?sici=0045-8511%2819741231%293%3A1974%3A4%3C990%3ATAEATB%3E2.0.CO%3B2-0>